A preliminary study of development in two *Latrodectus* species (Araneae: Theridiidae)

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Abstract

Young spiders of two New Zealand *Latrodectus* species were reared to maturity. Considerable variability in growth rate, instar length, relative size, colouration, and patterning was observed both intraspecifically and interspecifically. In general, successive instars increased in length. In both species males matured in 4 moults and lived for only 4-10 weeks, whereas females matured in 6 moults and often lived for 2 years.

Keywords: Araneae; Theridiidae; *Latrodectus katipo; Latrodectus atritus;* New Zealand; instars; development; variability; toxic to man.

INTRODUCTION

Spiders of the cosmopolitan genus *Latrodectus* are of considerable medical importance because of the potency of their venom to man. It is surprising, therefore, that there have been relatively few studies investigating the biology and behaviour of New Zealand representatives of this genus.

Although Ralph (1857) originally reported the presence of these spiders in this country, it was Powell (1871) who first described an adult female, naming it *Latrodectus katipo.* Urquhart (1885) mistakenly described a male spider as *Theridion melanozantha*; not until much later (Bryant 1933) was it correctly identified as *L. katipo.* Urquhart (1889) also described a female variant of *L. katipo* called *atritus* which differed from the typical form because of the absence of a red median stripe down the abdomen. At that time its range was believed to be limited but McCutcheon (1976) has since found that it is quite widely distributed around the North Island coasts.

After comparing a series of female *Latrodectus hasselti* from Tasmania with various specimens of the New Zealand *L. katipo,* Parrott (1948) came to the conclusion that these 2 forms are synonymous. Consequently, his view was that in New Zealand there is 1 species, *Latrodectus hasselti hasselti* Thorell (having a red abdominal stripe) and 1 subspecies, *Latrodectus hasselti atritus* (having no such stripe). Levi (1958) went further than this, postulating that since there were no conspicuous morphological differences between *L. hasselti* (New Zealand to India), *L. indistinctus* (Africa), *L. tredecimguttatus* (Mediterranean region), and *L. mactans* (North America), they all probably belonged to one species. Nevertheless, Forster & Forster (1973) adopted the view that *L. katipo* was a distinct species but that the form sometimes known as *L. atritus* was probably a variant of *L. katipo.*

More recent investigations however (R. R. Forster, in prep.) further support the original designation by Powell (1871) rather than the conclusions of Parrott (1948) and Levi (1958); these studies also show that *L. katipo* is quite distinct from *L. hasselti* and that it is endemic to this country. Moreover, behavioural studies (Kingsford & Forster, in prep.) suggest that *L. atritus* is not, in fact, a subspecies but a species in its own right.

This paper describes a preliminary study of development in these 2 species. Little was known of the breeding habits and life histories of these spiders in New Zealand when we began our investigations; hence some deficiencies in our methods resulted and some variations in feeding schedules occurred—these are noted in the text. In addition, it is now clear that rearing studies in which food and temperature are controlled would be useful and that a record of individual changes in colour and pattern might prove interesting—we hope that more rigorous investigations may be undertaken in the near future.

MATERIAL AND METHODS

Mature, fertile females were collected from 2 localities — a single *Latrodectus atritus* Urquhart from Bell Block, New Plymouth, Taranaki, and 4 *Latrodectus katipo* Powell, 1871 from Karitane Beach, Otago, in November 1979. They were housed in 1-pint Agee jars containing moistened cotton wool and 1 or 2 balsa wood sticks as a foundation for web construction. Two or 3 times a week they were fed with house flies.

Altogether 12 eggsacs were laid by *L. katipo* females and 3 by the *L. atritus* female over the summer period. One eggsac was taken from each species. In December 1979, 57 (out of 80) *L. katipo* spiderlings and 20 (the full complement) *L. atritus* spiderlings were separated for study. Upon emergence, spiderlings were placed in individually numbered vials (75 × 25 mm) containing moistened cotton wool and a balsa wood stick. Each vial was closed with a plastic stopper which had a small hole plugged with cotton wool. This simplified the introduction of prey and minimised disturbance of any web structures. Vials were kept in a box continuously illuminated by a 15-W bulb so as to maintain a temperature above 15°C during growth of the spiderlings. No attempt was made here to assess differential rates of growth as a function of temperature or prey consumption.

Twice a week *L. katipo* spiderlings were offered 3 or 4 vinegar flies (winged *Drosophila melanogaster*). Females were provided with house flies from the 4th instar, initially 1 a week but graduating to 2 during the 4th instar and thereafter. Males were given only 1 fly per week for the entire 4th instar. *Latrodectus atritus* were raised on a similar schedule but females were not offered 2 house flies until the 5th instar. Five (out of 10) males were given house flies in the 4th instar after it was noticed that earlier maturing males fed only with vinegar flies were short-lived (see Results). The cotton wool in each container was moistened with a few drops of water once a week.

In addition, 2 quart jars with 2 *L. katipo* eggsacs in each were set up in the same manner to observe the communal development of spiderlings. Appropriate quantities of prey, either *Drosophila* or house flies, depending on spider size, were introduced into these jars 2 or 3 times a week. Observations were usually restricted to these occasions since individual records were not possible.

Instar length is measured in days with values given as mean ± standard deviation. The 1st instar (egg to 1st moult) occurs in the eggsac; spiderlings emerge as 2nd instar individuals. Hence duration of the 2nd instar is recorded from emergence until the subsequent moult.

RESULTS

Spiders of both species proved relatively easy to maintain and rear in captivity so that, of the original complement of spiderlings, 96% reached maturity.

Prey-catching

After being isolated in single containers, neonatal spiderlings very quickly deposited several vertical strands of silk to which cross threads were added as they moved about. Once a suitable network had been established, they remained suspended and quiescent, usually in the upper portion of the container. Spiderlings became active when *Drosophila*, which had been introduced into their containers, flew into or walked along threads. Most spiderlings ran quickly towards the site of the disturbance and flies were rapidly immobilised when silk was thrown over them and they were bitten (see Herms et al. 1935; D'Amour et al. 1936; Court 1971, for details of prey capture).

In the community containers, spiderlings laid down threads as above, but in the course of time, a dense network of silk developed and the young spiders moved freely in this common web when *Drosophila* were introduced. The distance over which prey can be detected is apparently limited (up to about 4 cm) since usually only 4 or 5 spiderlings in the immediate vicinity were attracted to a *Drosophila* when it became caught in the web. Silk was thrown by all attendant spiderlings so that in a matter of seconds a *Drosophila* would be thoroughly enmeshed. It was not unusual, however, for a luckless spiderling also to be wrapped since silk-throwing tended to be rather indiscriminate under such circumstances.

As a consequence of this communal attraction to a particular prey item, competition developed over which spiderling was to eat the *Drosophila*. As one approached, another would drive it away, sometimes to the furthest corner of the web. Often all would-be consumers were engaged in chasing others away while the *Drosophila* was deserted.

Eventually one spiderling would succeed in establishing his 'right' to eat the prey although we were not able to determine how this 'right' was achieved. Not surprisingly, cannibalism was rife, at least initially, although the maturation of only 2 spiders (1 female and 1 male) in each cage most likely resulted from the failure of many of them to catch sufficient prey. We suspect that 'winners' of the 'right to consume' were also responsible for cannibalism but we were not able to verify this. However, D'Amour et al. (1936) observed that *L. mactans* spiderlings habitually fed upon each other after emerging and that the older, stronger ones persisted in cannibalising the younger ones. Baerg (1923) also noted that the young spiderlings fed upon their siblings even if flies and small grasshoppers were provided. We suggest, however, that cannibalism is the accidental consequence of competition for prey.

Compared to those *L. katipo* reared individually, the communally-bred spiders reached maturity earlier and were larger but nevertheless did not attain the size of wild spiders. Nutritional inadequacy is the most likely cause of the smaller-than-wild size in this instance since the fact that they reached maturity sooner than the individually reared spiders pre-supposes food sufficiency.

Feeding and development

The temperature at which eggsacs were maintained was not rigidly controlled but varied from about 15°-25°C; hatching time for the *L. atritus* eggsacs selected for this study was 40 days whereas for the *L. katipo* eggsac it was 30 days. When batches of *L. hasselti* eggs were subjected to a range of temperatures ($\leq$ 15°, 18°, 20°, 25°, 30°C), Downes (pers. comm.) found that at $\leq$ 15° there was no emergence, at 18° hatching occurred after 43 days but thereafter incubation times decreased quite substantially (34, 12, 10 days respectively) with higher temperatures. It seems likely that comparable results would be recorded for *L. katipo* and *L. atritus* under a similarly controlled regime except that the latter species might register a higher base value as suggested by the present results.

The decision to provide spiderlings with 6-8 *Drosophila* graduating to 2 house flies per week was an arbitrary one since there have been no detailed surveys of their prey consumption either in the wild or in captivity. Under this schedule however, they appeared healthy; there was only one death during moulting and 2 between moults. However, several *L. atritus* males which died within a few days of their final moult may have been victims of malnutrition (n = 5, mean longevity, 2.1 months). In contrast those males which were offered a house fly in their penultimate instar lived longer (n = 5, mean longevity 3.5 months).

Moulting almost invariably occurred at night and was usually established by the presence of fresh exuviae in the web. In some cases however, there was uncertainty about the date of moulting, hence our results are derived solely from those spiders for which we obtained accurate data. (Sample size is noted in figure captions.) Both *L. katipo* and *L. atritus* females reached maturity in 6 moults whereas males of both species were mature after 4 moults (including the pre-emergent moult).

A comparison of growth trends in females of both species (Fig. 1a, b) shows that, in general, successive instars increased in length. Note that these trends were apparently disrupted by a feeding discrepancy in the 4th instar (see Methods) when *L. atritus* spiders were offered fewer flies overall than *L. katipo,* with the result that duration of this instar was considerably extended in the former species compared to the latter. In both species, however, duration of the 5th instar was less than the previous one.

For males, the picture is similar (Fig. 1c, d). In *L. atritus* for instance, the growth pattern approximated that of females in having an aberrant 4th instar length. In *L. katipo,* the 4th instar more closely fitted the overall pattern, perhaps because these spiders had already been fed with house flies (see Methods) and had thus profited from the change of diet or actual food increase. Mean longevity is depicted in Fig. 1c, d.

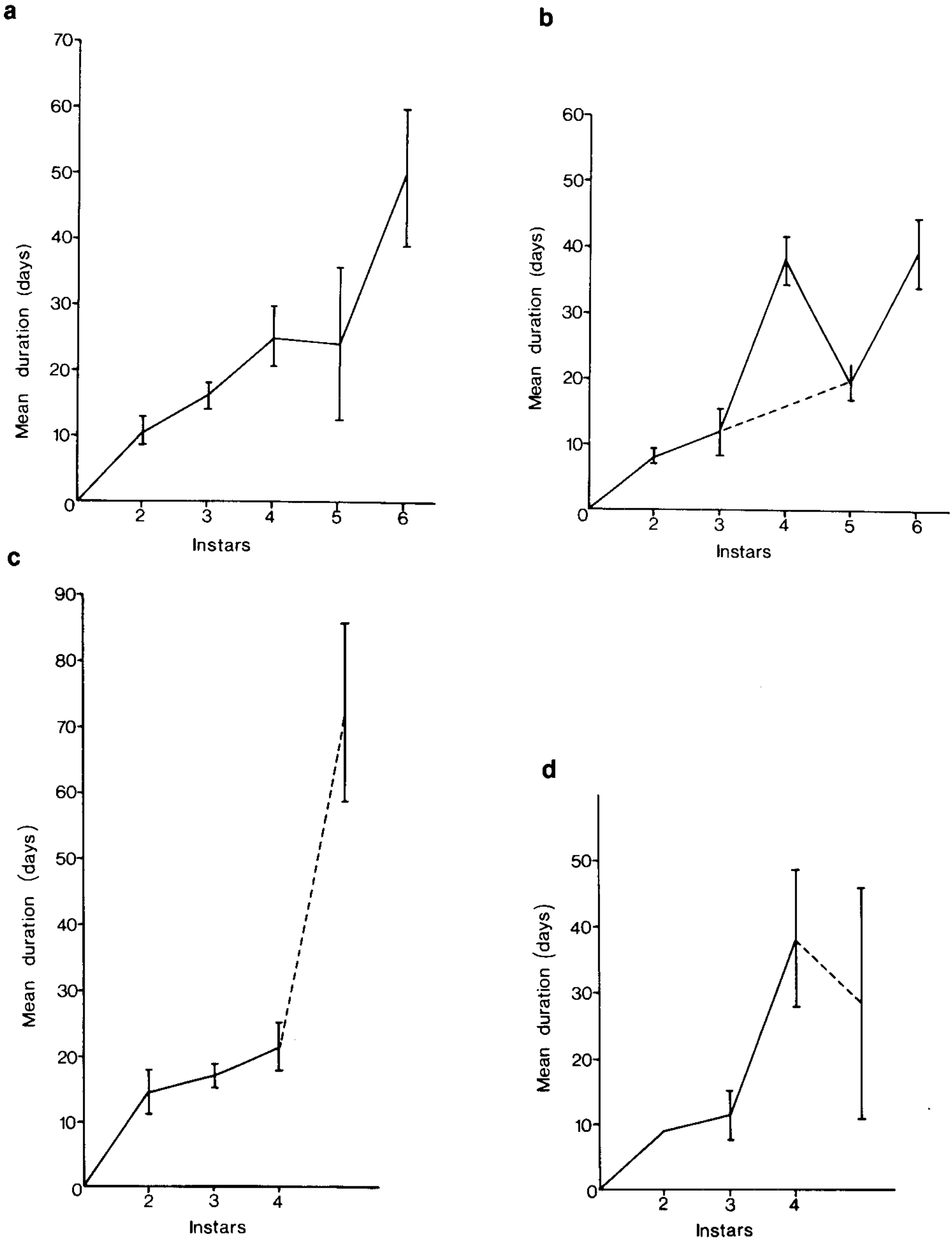

Fig. 1. Successive instars in *Latrodectus katipo* and *L. atritus* are plotted as a function of their mean duration and show an overall increase in length. Note that mean longevity is included for males (the number of days after the final moult) but not for females because of the latter's very much greater life span. Vertical bars represent standard deviation for each instar. (**a**) *L. katipo* females (n = 25): The fifth instar shows a slight decrease in instar length and greater variability about the mean than previous instars. (**b**) *L. atritus* females (n = 8): The fourth instar shows a substantial increase in length above earlier instars but this is followed by a corresponding drop in the subsequent instar (see text). (**c**) *L. katipo* males (n = 15): Instar duration shows a steady increase until maturity. Males lived for 72 ± 14 days after the 4th and final moult and did not catch prey during this time. (**d**) *L. atritus* males (n = 10): Instar length increased substantially during the 4th instar but spiders were relatively short-lived (28 ± 18 days) after the 4th and final moult (c.f. *L. katipo*). They did not catch prey after maturity.

In general, the effect of this feeding discrepancy was quite marked in *L. atritus* spiders, both males and females exhibiting greatly increased instar lengths for this period. However, a sharp decline in instar duration occurred in females when prey consumption returned to schedule. It could be argued that this situation compensated for the inordinately high values recorded for the previous instar particularly since the interpolated values (indicated by the broken line, Fig. 1b) between the 3rd and 5th instars support the view that normally a steady, but not excessive, increase in length occurs during successive instars.

A further supposition from these results is that instar length is a function of food intake, similarly demonstrated in *Trite auricoma* (Forster 1977) and suggested by Myashito (1968) in a study of *Lycosa T-insignata.* In a similar study, Deevey (1949) found that well-fed *L. mactans* spiders not only underwent fewer moults but matured in a shorter time than poorly-fed spiders.

Given that other instars reflected an adequate and relatively unvarying consumption rate, an interesting disparity in the time taken to maturity is revealed. Based on the date of emergence from eggsacs, females of both species took, on average, 17-18 weeks to reach adulthood, whereas males matured in much less time, viz., *L. katipo* in 7.5 weeks and *L. atritus* in 8 weeks. Since males live at most only a few weeks after maturity, one consequence of this developmental pattern is that most of them are unlikely to survive long enough to mate with siblings, thus reducing the likelihood of inbreeding; a similar conclusion was reached by Deevey & Deevey (1945) for *L. mactans.* In the laboratory, longevity for 'red-stripe' females was greater than for 'black', being about 2 years for the former and generally less than this for the latter. However, adult females, bred in the wild and then brought into the laboratory, often live longer than 2 years suggesting that dietary factors may influence longevity.

Figure 2 compares the mean and standard deviation (in days) for instar lengths of all 4 classes of spider (males, females, of the 2 species). Although the tendency for each species to exhibit disparate distributions is more marked in *L. artitus* in the 4th instar, it should be recalled that this period coincides with reduced food intake. Moreover it also constitutes the penultimate stage for males and as growth of the spider includes maturation of the reproductive organs (palps), there may be a valid physiological reason for this instar to be prolonged. A comparable situation pertains to females and, as the graphs (see Figs 1a, b & 2e) show, the 6th instar is prolonged. The present data do not allow further clarification of these aspects.

Inter-specific and intra-specific variability

Considerable variability in growth rate, instar length, relative size, colouration, and patterning was observed, not only between species but also amongst individual spiderlings of the same species. No detailed records were kept of such variations but it was apparent, when abdominal features were closely scrutinised that one spiderling, for example, might show a greater area of reddish-orange markings than another, or that such markings were paler or darker. In some instances, the black lateral stripes and diamond-shaped dorsal patterns were quite distinctive, in others they were reduced and discontinuous, and so on. These differences were much more pronounced when the 2 species were compared but they were also readily observed amongst spiderlings of the same species and even in the same instar for example. Successive moults led to further changes in each spiderling. It would be of interest to follow such individual characteristics through to the mature spider to see whether any particular features are reflected in the adult markings.

In *L. katipo,* adult females possess a red, dorsal, abdominal stripe, a distinctive feature which is missing in *L. atritus* females. This diamond-shaped stripe, a legacy of the juvenile stage, varies in the details of its shape, intensity of colour, and other associated marking. *Latrodectus atritus* spiders have similar reddish diamond-shaped

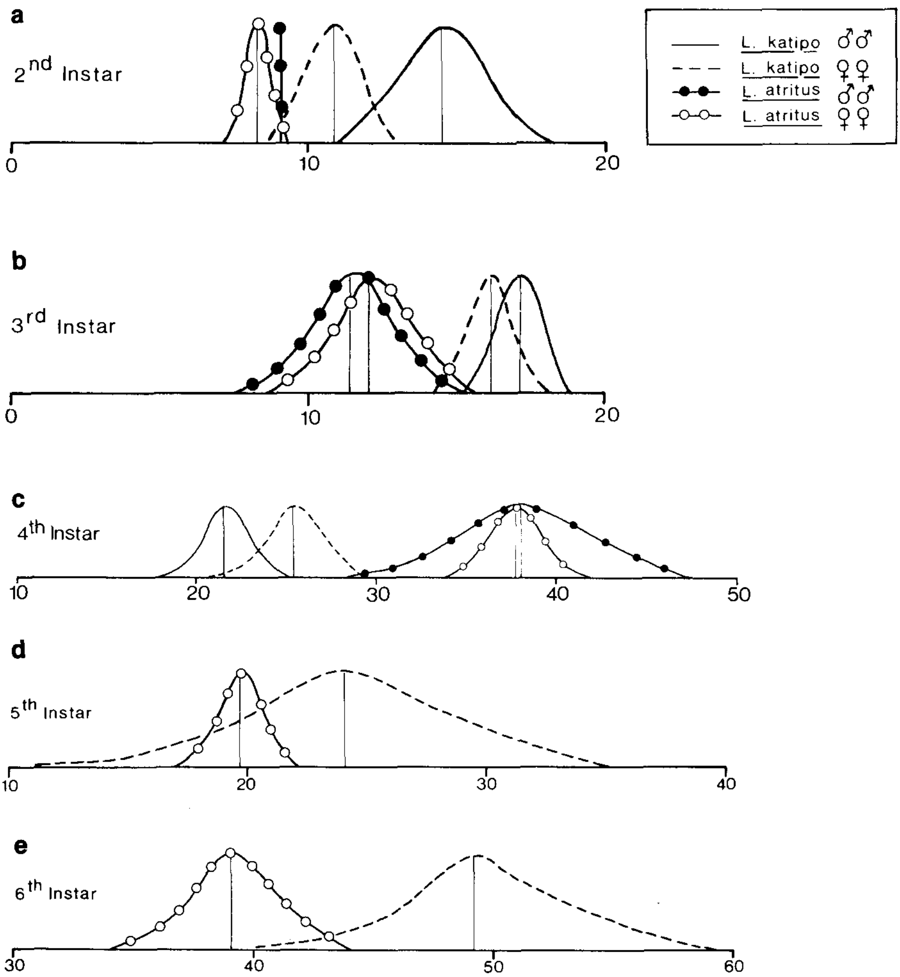

Fig. 2. The distribution of instar length about the mean (one standard deviation) is compared for each instar in *Latrodectus katipo* and *L. atritus*, males and females. (**a**) 2nd instar: Higher mean values and a greater distribution about these means distinguish *L. katipo* from *L. atritus*. (**b**) 3rd instar: Mean values and distribution about means are comparable for males and females in each species. (**c**) 4th instar: In: *L. atritus*, this instar is characterised by higher mean values and greater variability about the mean.

Since males are now mature only females are compared in d and e. (**d**) 5th instar: Variability in *L. katipo* females is greater than for *L. atritus* but this might serve to compensate for the reverse situation in the previous instar. (**e**) 6th instar: Differences between the 2 species in this instar are in keeping with inconsistencies apparent in all of the later instars. A number of factors may account for this variability (see text).

markings during the juvenile stages but these gradually fade, disappearing entirely in the adult female.

Superficially, there is less distinction between the adult males of the 2 species. Both are about one-sixth the size of their respective females, and more closely resemble juveniles. However, we observed that, in *L. atritus* males, colours and patterns were paler and generally less continuous; areas which were black in *L. katipo* tended towards brown in *L. atritus,* and the dark red stripe of the former species appeared as light orange in the latter.

Except for the instance already noted, food was supplied regularly although the number of *Drosophila* varied from 3-4 items, this being largely determined by the availability or sometimes the size of the prey items to be presented. Generally the same number of flies were offered to all spiderlings at a particular feeding, but it was not known whether all flies were always consumed, hence we have no precise measure of prey consumption.

Assuming, however, that the spiderlings were adequately fed (and the fact that such a high proportion reached maturity seems to bear this out), then we must conclude that differences in the growth rate of spiderlings are due in part to some intrinsic physiological differences. If, for example, we compare the records for spiderling number 13 which reached maturity in 103 days with spiderling number 30 which reached maturity in 159 days, we see that for number 13 instar lengths were always less than the mean, whereas for number 30 they were equal to (in one case) or greater than the mean. Since, on average, all spiderlings had access to the same number of flies, this suggests that either they voluntarily consumed differing quantities, or that they ate the same amount but their metabolic rates were inherently different.

DISCUSSION

From our laboratory observations as well as those of D'Amour et al. (1936) and Kaston (1968) it seems likely that, in the wild, *Latrodectus* spiderlings feed upon each other in the early days of their lives although no doubt they also trap small insects found among the vegetation. Differential growth rates may lead to differences in the kind and size of prey hunted, perhaps reducing competition and cannibalism.

Our observations also suggest that food consumption is important in determining instar length and hence time to maturity, while studies by Downes (pers. comm.) support the view that temperature is a key factor governing instar length. No doubt both variables play a part but carefully controlled tests are needed to determine their relative significance.

Periods of time to maturity for females (17-18 weeks) and males (7.5-8 weeks) for *L. katipo* and *L. atritus* are consistent with the average values recorded in captivity for *L. mactans* (Herms et al. 1935) and in the field for *L. indistinctus* (Smithers 1944). However, studies by McCrone & Levi (1964) and Kaston (1970) show that there is considerable individual variability in *L. mactans* in the time taken to reach maturity even under uniform environmental conditions. Whereas we found no difference in the number of moults to maturity for any spider, in either species, Herms et al. (1935), Smithers (1944), and Kaston (1970) note that total moults vary from 4 to 9, both inter- and intra-specifically, in the species mentioned above.

We noted much variability in colouration and patterning. Similar variability has been recorded for other *Latrodectus* species; Reese (1940), for instance, found that of 36 black widow spiderlings examined, only 2 were so similarly marked as to appear practically identical, while Kaston (1970) reported wide variation in appearance among both juveniles and adults in *L. mactans, L. variolus,* and *L. hesperus.* Indeed there is overwhelming support for the notion of variability in all aspects of the life cycle of most *Latrodectus* species, ranging from the number of moults, interval between moults, longevity, colour, and patterning, not only between species but also among 'litter-mates' (see Kaston 1970). Perhaps the key to the world-wide distribution of this genus lies in this variability, as a consequence of which, spiders adjust their life cycles to changing environmental parameters as they arise.

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